

AGROCLIMATOLOGY

Interactive Effects of Carbon Dioxide and Nitrogen Nutrition on Cotton Growth, Development, Yield, and Fiber Quality

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ABSTRACT

The consequences of elevated carbon dioxide concentrations ($[\text{CO}_2]$) and N nutrition on cotton (*Gossypium hirsutum* L.) growth, development, yield, and fiber quality were determined. Cotton cultivar NuCOTN 33B was grown in sunlit controlled environment chambers at three levels of $[\text{CO}_2]$ (180, 360, and 720 $\mu\text{mol mol}^{-1}$) and two levels of N [continuous N throughout the plant growth period (N+) and N withheld from flowering to harvest (N-)]. Leaf N concentration decreased with increasing $[\text{CO}_2]$ under both N treatments. These low leaf N concentrations did not decrease the effect of elevated $[\text{CO}_2]$ in producing higher lint yields at both N treatments, the response being highest for plants grown at elevated $[\text{CO}_2]$ and N+ conditions. Fiber quality was not significantly affected by $[\text{CO}_2]$, but the leaf N concentrations, which varied with $[\text{CO}_2]$, had either a positive or a negative influence on most of the fiber quality parameters. Leaf N during boll maturation period had significant positive correlations with mean fiber length ($r^2 = 0.63$), fine fiber fraction ($r^2 = 0.67$), and immature fiber fraction ($r^2 = 0.65$) and negative correlations with mean fiber diameter ($r^2 = 0.61$), short fiber content ($r^2 = 0.50$), fiber cross-sectional area ($r^2 = 0.76$), average circularity ($r^2 = 0.74$), and micronafis ($r^2 = 0.65$). It is inferred that future elevated $[\text{CO}_2]$ will not have any deleterious effects on fiber quality and yield if N is optimum. The developed algorithms, if incorporated into process-level crop model, will be useful to optimize cotton production and fiber quality.

GLOBAL ATMOSPHERIC $[\text{CO}_2]$ has risen by more than 30% since the preindustrial times, from about 280 $\mu\text{mol mol}^{-1}$ to the current levels of 370 $\mu\text{mol mol}^{-1}$ (Houghton et al., 2001). If current anthropogenic CO_2 emissions rates continue in the future, the most recent future scenarios of greenhouse gases in the atmosphere indicate that atmospheric $[\text{CO}_2]$ could increase from current levels to between 540 and 970 $\mu\text{mol mol}^{-1}$ by the end of the 21st century (Houghton et al., 2001). With concern over maintaining cotton fiber production in the future environments, experiments on elevated $[\text{CO}_2]$ have been conducted in cotton (Kimball and Mauney, 1993; Mauney et al., 1994; Pinter et al., 1996; Reddy et al., 2000). Techniques used varied from controlled-environment, open-top chambers to the application of free-air CO_2 enrichment (FACE) facilities. Results from sun-lit chambers showed that a 100% increase in $[\text{CO}_2]$

from ambient levels of 360 $\mu\text{mol mol}^{-1}$ increased vegetative biomass by 40% and boll biomass by 20% (Reddy et al., 1997). Open-top chamber experiments (Kimball and Mauney, 1993) showed that elevated $[\text{CO}_2]$ of 650 $\mu\text{mol mol}^{-1}$ increased the aboveground biomass by 63% and seed cotton yield by 60% compared with plants grown at ambient $[\text{CO}_2]$. Similarly, results from FACE experiments showed that CO_2 enrichment (550 $\mu\text{mol mol}^{-1}$) produced 35% more biomass and 60% more lint yield compared with plants grown at ambient atmospheric $[\text{CO}_2]$ (Mauney et al., 1994; Pinter et al., 1996). Generally, increasing atmospheric $[\text{CO}_2]$ is shown to have a stimulatory effect on plant biomass production as a consequence of the rise in net photosynthesis (Bazzaz, 1990; Poorter, 1993, 1998). Although a strong response of cotton yield to future CO_2 increases was observed, other environmental factors are shown to modify this response (Poorter and Perez-Soba, 2001).

The response of agricultural crops to future climate change also depends on management practices. One key environmental factor is nutrient availability, which is an important factor influencing the extent of CO_2 response of the plants (Poorter, 1998). Under field conditions, nutrients, particularly N, are often scarce. This may lead to intensification of competition of resources under elevated $[\text{CO}_2]$ (Zanetti et al., 1997). Increased rates of growth in elevated $[\text{CO}_2]$ will normally lead to increased demand for all mineral nutrients. It is important to address whether the lint quality of cotton, the world's foremost important fiber crop, will be affected by higher atmospheric $[\text{CO}_2]$ in interaction with other growth-limiting major nutrients such as N.

Interaction of atmospheric $[\text{CO}_2]$ and N nutrition on cotton growth and development was previously addressed in several short-duration experiments (Wong, 1979; Rogers et al., 1993, 1996a, 1996b; Conroy and Hocking, 1993), which showed changes in nutritional physiology of the crop with elevated $[\text{CO}_2]$. However, there are still basic questions on how plants will respond to elevated atmospheric $[\text{CO}_2]$ when nutrients are limiting (Bazzaz and Catovsky, 2002; Poorter and Navas, 2003; Lloyd and Farquhar, 2000). The number of studies on the influence of $[\text{CO}_2]$ on lint yield and fiber quality is limited. Atmospheric $[\text{CO}_2]$ and temperature effects on

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Abbreviations: AFIS, advanced fiber information system; A(n), average cross-sectional area of the fiber; BMP, boll maturation period; $[\text{CO}_2]$, carbon dioxide concentration; DAE, days after emergence; FACE, free-air CO_2 enrichment; FFF, fine fiber fraction; IFF, immature fiber fraction; leaf N-BMP, leaf nitrogen during boll maturation period; N+, continuous nitrogen throughout the plant growth period; N-, nitrogen withheld from flowering to harvest; SFC, short fiber content; SPAR, soil-plant-atmosphere research; θ , average circularity of the fiber; μAFIS , micronafis.

cotton yield and fiber quality have been addressed to certain extent (Reddy et al., 1999). They showed that atmospheric $[\text{CO}_2]$ had no significant effect on cotton fiber, but high temperatures had a negative influence on some important fiber parameters. The N nutrition effect on certain fiber properties has been studied (Koli and Morrill, 1976; Rochester et al., 2001). Some studies found that N nutrition increased both lint yield and fiber length, implying that N deficiency would reduce fiber length below what may be acceptable to the industry (Constable and Hearn, 1981; Hearn, 1976). Some other studies concluded that N nutrition does not affect any of the fiber quality parameters (Bowman and Westerman, 1994; Murray et al., 1965). The interaction of $[\text{CO}_2]$ and N nutrition on cotton fiber quality has not been studied so far.

Comprehensive crop simulation models are needed to address climate change projections on cotton growth, development, and lint yield and quality. To date, there are no predictive models to predict fiber quality as affected by environmental factors (Bradow and Davisonis, 2000; Reddy et al., 2002b). The cotton simulation models that have been successfully used as on-farm simulation decision aids to optimize production practices (Hearn, 1994a; McKinion et al., 1989; Plant, 1989; Reddy et al., 2002b) lack the capabilities to simulate fiber properties.

The objectives of this study were to investigate the combined effects of $[\text{CO}_2]$ and N nutrition on yield and fiber quality of cotton. Our specific objectives were to (i) evaluate effects of atmospheric $[\text{CO}_2]$ on leaf N concentrations and yield attributes of cotton grown under N+ and N- conditions; (ii) study interactive effects of $[\text{CO}_2]$ and N on cotton growth, development, lint yield, and fiber quality under optimum water and temperature conditions; and (iii) provide functional algorithms for fiber quality as affected by C and N to develop fiber quality models.

MATERIALS AND METHODS

Soil-Plant-Atmosphere Research Chambers

The experiment was conducted in six sunlit soil-plant-atmosphere research (SPAR) chambers at Mississippi Agricultural and Forestry Experiment Station, Mississippi State (33°28' N, 88°47' W), MS, USA. Each SPAR chamber consists of a steel soil bin (1.0 m deep by 2.0 m long by 0.5 m wide) to accommodate the root system, a Plexiglas chamber (2.5 m tall by 2.0 m long by 1.5 m wide) to accommodate aerial plant parts, a heating and cooling system, and an environmental monitoring and control system. Chamber temperature and $[\text{CO}_2]$ can be controlled at predetermined set points. The Plexiglas transmits $96.6 \pm 0.5\%$ of the incoming photosynthetically active radiation (400 to 700 nm). During the experiment, the average daily total solar radiation outside the SPAR chambers, measured with a pyranometer (Model 4-48, The Epply Laboratories Inc., Newport, RI, USA), was $19.7 \pm 0.39 \text{ MJ m}^{-2} \text{ d}^{-1}$. The total daily solar radiation levels during the experiment, however, ranged from 6.3 to $27.8 \text{ MJ m}^{-2} \text{ d}^{-1}$, and only 15 d of the total 138-d experimental period had solar radiation levels less than $10 \text{ MJ m}^{-2} \text{ d}^{-1}$.

The heating and cooling devices were connected by air ducts located on the northern side of each SPAR chamber.

Conditioned air was passed from above through the plant canopy with sufficient speed to cause leaf flutter (4.7 km h^{-1}) and was returned to the air-handling unit just above the soil level. Chilled ethylene glycol was supplied to the cooling system via several parallel solenoid valves that opened or closed depending on the cooling requirement. To fine-tune the air temperature, as and when needed, two electrical resistance heaters provided short pulses of heat. Chamber air temperature, $[\text{CO}_2]$, and soil watering in each SPAR chamber were controlled by a dedicated computer system (Digital Pro 380, Digital Equipment, Maynard, MA, USA), which continuously monitors all the important environmental and plant gas exchange variables. Additional description of the SPAR chambers, their control, and operation has been reported by Reddy et al. (2001).

Plant Culture

Seeds of cotton cultivar NuCOTN 33B, a midseason Upland Bt variety, were sown on 16 June 1998 in the soil bins of SPAR chambers that were filled with fine sand. Each SPAR chamber had three rows of five plants each, with each row 0.67 m apart. Emergence was observed 4 d later. Variable-density shade cloths placed around the edges of plants at emergence were adjusted regularly to match plant heights, simulating the presence of other plants and minimizing the need for border plants.

Temperature, Carbon Dioxide, and Nitrogen Treatments

The temperature in the chambers was monitored at 10-s intervals and was maintained at $30/22^\circ\text{C}$ (day/night) throughout the experiment in all SPAR chambers. The daytime temperature was initiated at sunrise and returned to nighttime temperature 1 h after sunset. The average temperature recorded during the experimental period in all SPAR chambers was $26.63 \pm 0.04^\circ\text{C}$. The $[\text{CO}_2]$ in each SPAR chamber was also monitored at 10-s and integrated over 900-s intervals throughout the day. The plants were grown at three $[\text{CO}_2]$ levels, subambient $[\text{CO}_2]$, ambient $[\text{CO}_2]$, and elevated $[\text{CO}_2]$ starting from emergence. The $[\text{CO}_2]$ levels recorded were $178.5 \pm 0.36 \mu\text{mol CO}_2 \text{ mol}^{-1}$ for subambient $[\text{CO}_2]$, $360.8 \pm 0.79 \mu\text{mol CO}_2 \text{ mol}^{-1}$ for ambient $[\text{CO}_2]$, and $718.7 \pm 0.70 \mu\text{mol CO}_2 \text{ mol}^{-1}$ for elevated $[\text{CO}_2]$ measured on a clear, sunny day during the midfruiting period. As the SPAR system doesn't have CO_2 venting systems, the chamber $[\text{CO}_2]$ at the subambient $[\text{CO}_2]$ treatment was higher than the treatment set point during the morning hours and on few cloudy days during the experiment.

A half-strength Hoagland's nutrient solution was supplied, three times a day, to each growth chamber via drip irrigation system. At initial flowering, 45 d after emergence (DAE), the SPAR soil bins were leached with water, and in each of the $[\text{CO}_2]$ treatments, one chamber had a continuous supply of half-strength Hoagland nutrient solution throughout the growth period (N+) and the other without nitrogen (N-) until harvest (Reddy et al., 1996).

Measurements

Plant height from the cotyledonary node to the newest unfolded mainstem leaf at final harvest was measured. The number of nodes on the mainstem was also recorded. Flowers and open bolls were tagged daily in all the units on all the plants throughout the duration of the experiment. The day of anthesis (appearance of white flower) and day of boll dehiscence (cracking of the boll and appearance of lint) were

marked on the same tag. Abscised bolls were collected and counted daily. At the time of final harvest, 138 DAE, the numbers of fruiting sites and bolls produced and retained were counted on all the plants. Boll maturation period (BMP) was calculated as the time taken from the day of anthesis to day of boll dehiscence.

Branch (vegetative and fruiting) numbers and lengths were counted and measured along with the number of fruiting sites on all 15 plants at final harvest. Leaf, stem (including branches), and root weights were recorded at the final harvest. Root weights were obtained by extracting the roots of all 15 plants by excavating the entire soil bin of the chamber, passing through a sieve, and drying to constant weight. Bolls were separated into burr, lint, and seed and then weighed. Seeds in each boll were counted. Leaf N concentrations were estimated at 7-d intervals from flowering in the topmost fully expanded leaves by the micro-Kjeldahl digestion method (Nelson and Sommers, 1972). Daily leaf N was calculated from weekly leaf N by regression techniques. Leaf N during BMP (leaf N-BMP) was the average of daily leaf N during the BMP.

Fiber Analysis

Based on the flowering dates, open bolls were divided into seven groups. The bolls developed from the flowers that were produced in the first week of flowering constituted the first group. Similarly, seven groups of bolls were classified by week in every treatment. All bolls from all seven groups were analyzed individually for the fiber quality parameters. Advanced fiber information system (AFIS) (Zellweger Uster Inc., Knoxville, TN, USA), equipped with a length and a diameter module and a fineness and maturity module, was used to measure fiber quality parameters as described by Davidonis and Hinojosa (1994) and Bradow et al. (1994). Samples of fibers from each week of flowering were taken from the middle seeds of each locule, and fiber analysis was performed on a per-boll basis. During the analysis, the fibers were combed, separated, and transported in a high-speed air stream perpendicular to an electron ribbon of light directed to an electron-optical sensor (Bragg and Shofner, 1993; Wartelle et al., 1995; Davidonis et al., 1996). The light blocked by an individual fiber is directly proportional to its mean diameter (Bragg and Shofner, 1993). The extinction mode signal data provided fiber length by weight and fiber diameter data. The short fiber content (SFC), i.e., percentage of fibers <12.7 mm, was generated from fiber length histograms as described by Reddy et al. (1999).

As the fiber moved with the air stream, part of the beam was scattered, reducing the amount of undeflected light and increasing the light at a specified scattering angle (40°). The scatter mode signal was analyzed to determine the average fiber cross-sectional area [$A(n)$] and average circularity (θ) of the fiber. The immature fiber fraction (IFF) was the percentage of the fibers with θ values <0.25. The fine fiber fraction (FFF) was obtained from the distribution of $A(n)$ and represents the percentage of fibers with $A(n) < 60 \mu\text{m}^2$. Micronafis (μAFIS) is AFIS-calculated micronaire that is closely correlated with micronaire (Davidonis and Hinojosa, 1994; Bradow and Davidonis 2000) and was also measured on individual bolls. Mean AFIS sample size in this study was 10 000 fibers per assay.

Statistical Analysis

The SPAR chambers were designed identically to provide uniform growth conditions, and the treatments under study were finely controlled. All the measurements measured on 15 plants in each treatment were used as replications for testing

the significance of treatments, and standard errors are provided in the tables and figures. The data on growth, dry matter, and boll parameters were analyzed by ANOVA procedures in GENSTAT 6 for Windows (Genstat 6 Committee, 1997) to determine the main and interactive effects of $[\text{CO}_2]$ and N. Boll retention percentages were subjected to angular transformations before statistical analysis. Regressions were fitted for leaf N concentrations by plotting against days after treatment for all the treatments. Differences between the treatments were determined by testing the heterogeneity of slopes and comparison of intercepts (Curnow et al., 2001) by Genstat 6 for Windows. For fiber parameters, measurements were made on individual bolls from seven groups in each treatment, and the standard errors are provided in the tables and figures. Individual bolls in each group were treated as replications for testing the significance of treatments. Regression analysis by Genstat 6 for Windows was used to examine the fit between leaf N-BMP and the fiber quality parameters.

RESULTS

Leaf Nitrogen Concentrations

Regression analysis showed that leaf N concentrations differed significantly between N and CO_2 levels ($P < 0.001$) (Fig. 1). The decline in leaf N was much steeper for elevated $[\text{CO}_2]$ -grown plants (slope: -0.408) compared with plants grown at ambient $[\text{CO}_2]$ (slope: -0.404) and subambient $[\text{CO}_2]$ (slope: -0.36) (Fig. 1). On an average, the decrease in leaf N concentrations due to N- treatment was higher under elevated $[\text{CO}_2]$ (39%) than ambient $[\text{CO}_2]$ (29%) and subambient $[\text{CO}_2]$ (11%) conditions. Compared with plants grown at subambient $[\text{CO}_2]$, elevated $[\text{CO}_2]$ -grown plants showed 18 and 43% lower leaf N concentrations under N+ and N- conditions, respectively.

Plant Growth and Development

No significant interactions between $[\text{CO}_2]$ and N were observed for plant height and mainstem nodes (Table 1). Both the parameters increased significantly ($P < 0.05$) with increasing $[\text{CO}_2]$ levels. Nitrogen levels did not significantly affect the plant height and mainstem nodes. At the final harvest, 138 DAE, plants grown at elevated $[\text{CO}_2]$ were significantly taller by 36 and 19% than the plants grown at subambient $[\text{CO}_2]$ at both N+ and N- conditions, respectively. Similar responses were observed for the mainstem nodes, where the increases were 30 and 11% for plants grown at elevated $[\text{CO}_2]$ compared with subambient $[\text{CO}_2]$ -grown plants at both N+ and N- conditions, respectively (Table 1).

Significant $[\text{CO}_2]$ and N interactions were observed for number of vegetative and fruiting branches, length of vegetative branches, and average number of fruiting sites on vegetative branches (Table 2). Out of the six treatments, plants grown at elevated $[\text{CO}_2]$ and N+ conditions produced more branches (both vegetative and fruiting) and more fruiting sites on the vegetative branches. Branch lengths and fruiting sites were significantly higher (33 and 27%) for the plants grown in elevated $[\text{CO}_2]$. Plants grown at N+ conditions produced significantly more (27%) fruiting sites than plants grown at N- conditions. Plants grown at N+ conditions produced more

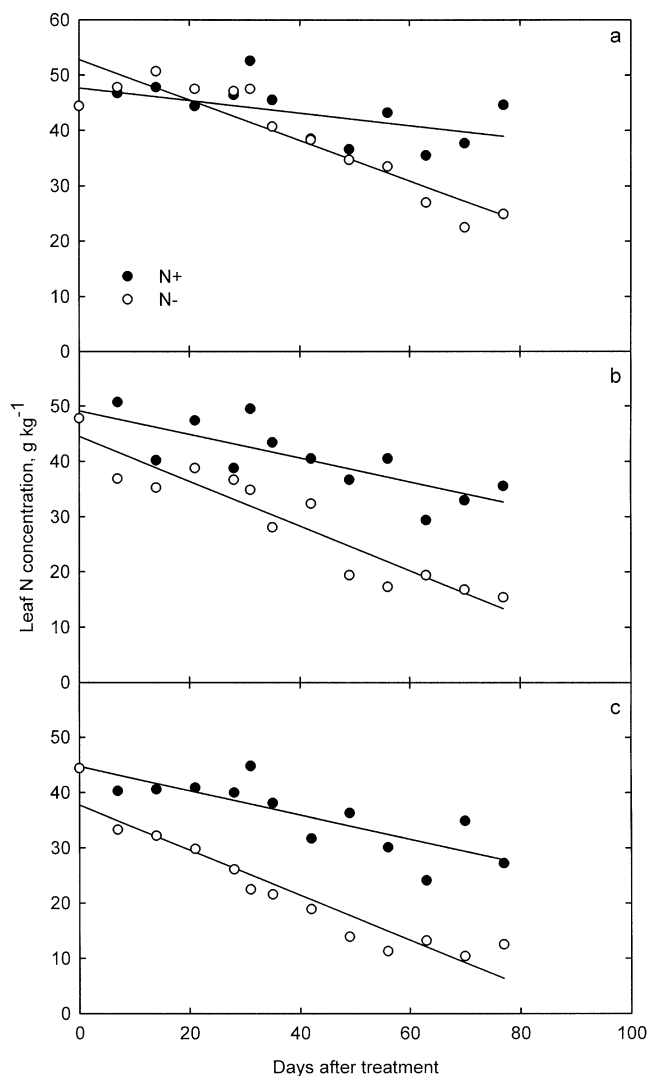


Fig. 1. Temporal trends in cotton leaf N concentrations as influenced by N and atmospheric carbon dioxide concentrations ($[CO_2]$). Fitted regressions are (a) subambient $[CO_2]$: $y = -0.113 (\pm 0.052)x + 47.65 (\pm 2.3)$, $r^2 = 0.30$ for N+ (N supplied throughout the plant growth period) and $y = -0.36 (\pm 0.048)x + 52.81 (\pm 0.215)$, $r^2 = 0.84$ for N- (N withdrawn from nutrient solution from flowering to harvest) treatments; (b) ambient $[CO_2]$: $y = -0.21 (\pm 0.049)x + 49.14 (\pm 2.1)$, $r^2 = 0.63$ for N+ and $y = -0.404 (\pm 0.045)x + 44.52 (\pm 2.02)$, $r^2 = 0.88$ for N-; and (c) elevated $[CO_2]$: $y = -0.22 (\pm 0.046)x + 44.74 (\pm 2.04)$, $r^2 = 0.68$ for N+ and $y = -0.408 (\pm 0.041)x + 37.77 (\pm 1.82)$, $r^2 = 0.90$ for N- treatments.

fruiting sites and retained more bolls on all fruiting branches (Table 3).

A significant $[CO_2] \times N$ interaction was observed for total bolls produced ($P < 0.001$) and retained ($P < 0.05$). The bolls produced and retained per plant were significantly higher for the plants grown at elevated $[CO_2]$ and N+ conditions than the other treatments. Plants grown at ambient $[CO_2]$ and N+ condition and elevated $[CO_2]$ and N- condition performed similarly for total bolls produced and retained (Table 3). Percentage boll retention did not differ significantly due to atmospheric $[CO_2]$, whereas significant differences ($P < 0.001$) were observed due to N treatment. Atmospheric $[CO_2]$ did not have any effect on days to flower, and all

Table 1. Plant height and mainstem nodes measured at 138 d after emergence on cotton plants grown at subambient, ambient, and elevated levels of carbon dioxide concentration ($[CO_2]$) (180, 360, and 720 $\mu\text{mol mol}^{-1}$, respectively) at two levels of N [continuous N throughout the plant growth (N+) and N withheld from flowering (N-)]. Values are means \pm standard error, $n = 15$.

Treatments		Plant height	Mainstem nodes
N	$[CO_2]$	cm	no. plant ⁻¹
N+	Subambient	145.8 \pm 2.6	19.1 \pm 2.6
	Ambient	180.5 \pm 6.5	23.2 \pm 0.82
	Elevated	198.8 \pm 6.2	25.2 \pm 0.62
N-	Subambient	156.7 \pm 4.9	20.3 \pm 0.44
	Ambient	182.1 \pm 5.2	22.1 \pm 0.35
	Elevated	185.5 \pm 6.2	22.4 \pm 0.47
ANOVA			
$[CO_2]$		**	*
N		NS†	NS
$[CO_2] \times N$		NS	NS

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† NS, not significant at the 0.1 probability level.

the treatments took 45 d to flower. Boll maturation period in elevated $[CO_2]$ -grown plants was 47 d, whereas in subambient $[CO_2]$ -grown plants, it was extended by about 3 d. Nitrogen levels did not affect the BMP.

Dry Matter Accumulation and Partitioning

There were no interactions between $[CO_2]$ and N for total or individual-component dry weights (Table 4). However, significant $[CO_2]$ and N main effects were observed for those traits. Plants grown at elevated $[CO_2]$ treatment produced significantly more total biomass (93%) and more total boll weights (52%) compared with plants grown at subambient $[CO_2]$ conditions (Table 4). Plants grown at N+ conditions produced significantly more total biomass (19%) and more total boll weights (21%) than plants grown at N- conditions. Significant increases in root biomass were observed with increasing $[CO_2]$ levels (72%). Plants grown at N- conditions produced significantly more root biomass (13%) than plants grown at N+ conditions. With higher $[CO_2]$ treatments, the root/shoot ratio decreased significantly from 0.071 at subambient $[CO_2]$ to 0.066 at ambient $[CO_2]$ and to 0.063 at elevated $[CO_2]$.

Significant $[CO_2] \times N$ interactions were observed for individual boll and seed weight and seed number per boll (Table 5). Plants grown at subambient $[CO_2]$ and N+ conditions had significantly greater boll weight compared with plants grown at other treatments. Atmospheric $[CO_2]$ levels differed significantly for seed weight, and no significant $[CO_2]$ effect was observed for other individual boll and boll-component (burr and lint) weights and seed number per boll. Boll weight and seed and lint weights per boll significantly differed between N+ and N- conditions (Table 5). Plants grown at N+ conditions had significantly greater boll weights and seed weights per individual bolls compared with plants grown at N- conditions.

Relationship between Leaf Nitrogen Concentrations and Fiber Quality Parameters

There were no significant effects of atmospheric $[CO_2]$ on any of the fiber parameters observed for plants grown

Table 2. Vegetative and fruiting branch numbers, average branch lengths, and number of fruiting sites on these branches measured at 138 d after emergence on cotton plants grown at subambient, ambient, and elevated levels of carbon dioxide concentration ($[CO_2]$) (180, 360, and 720 $\mu\text{mol mol}^{-1}$, respectively) at two levels of N [continuous N throughout the plant growth (N+) and N withheld after flowering (N-)]. Values are means \pm standard error, $n = 15$.

Treatments		Vegetative branches			Fruiting branches		
N	$[CO_2]$	Number	Length	Fruiting sites	Number	Length	Fruiting sites
		no. plant ⁻¹	cm branch ⁻¹	no. branch ⁻¹	no. plant ⁻¹	cm branch ⁻¹	no. branch ⁻¹
N+	Subambient	4.4 \pm 1.07	42.4 \pm 6.29	8.6 \pm 2.2	19.5 \pm 0.83	19.5 \pm 1.7	3.0 \pm 0.23
	Ambient	1.3 \pm 0.25	39.4 \pm 6.02	8.1 \pm 1.2	20.9 \pm 0.47	31.2 \pm 1.6	4.5 \pm 0.38
	Elevated	7.4 \pm 1.09	48.3 \pm 6.88	8.7 \pm 2.0	22.9 \pm 1.4	29.5 \pm 2.6	4.1 \pm 0.2
N-	Subambient	2.6 \pm 0.28	47.0 \pm 5.9	5.7 \pm 1.2	14.8 \pm 0.94	21.9 \pm 2.3	2.4 \pm 0.22
	Ambient	1.1 \pm 0.36	68.0 \pm 9.2	7.7 \pm 1.2	17.5 \pm 1.2	31.7 \pm 2.5	3.3 \pm 0.2
	Elevated	2.9 \pm 0.67	63.0 \pm 9.1	6.1 \pm 0.71	17.8 \pm 1.1	32.4 \pm 2.8	3.3 \pm 0.82
ANOVA	$[CO_2]$	*	***	NS†	*	***	***
	N	*	***	*	*	NS	***
	$[CO_2] \times N$	***	***	**	***	NS	NS

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† NS, not significant at the 0.1 probability level.

at N+ conditions. However, irrespective of atmospheric $[CO_2]$ conditions, fiber quality parameters had significant positive/negative correlations with leaf N-BMP. Therefore, functional algorithms were developed between leaf N-BMP and fiber quality parameters.

Leaf N-BMP had significant positive correlation with mean fiber length ($r^2 = 0.63$; $P < 0.001$) (Table 2a) and negative correlations with mean fiber diameter ($r^2 = 0.61$; $P < 0.001$) (Table 2b) and SFC ($r^2 = 0.50$; $P < 0.001$) (Table 2c). Fiber maturity parameters such as μAFIS ($r^2 = 0.65$; $P < 0.001$) (Table 3a), A(n) ($r^2 = 0.76$; $P < 0.001$) (Table 3b), and θ ($r^2 = 0.74$; $P < 0.001$) (Table 3c) followed a significant negative trend with leaf N-BMP. The leaf N-BMP had significant positive correlations with fineness parameters such as FFF ($r^2 = 0.67$; $P < 0.001$) (Table 4a) and IFF ($r^2 = 0.65$; $P < 0.001$) (Table 4b).

DISCUSSION

With increasing $[CO_2]$, significant sequential decreases in leaf N concentrations per unit dry mass from

Table 3. Total bolls produced and retained and the percentage retention of bolls of cotton plants grown at subambient, ambient, and elevated levels of carbon dioxide concentration ($[CO_2]$) (180, 360, and 720 $\mu\text{mol mol}^{-1}$, respectively) at two levels of N [continuous N throughout the plant growth (N+) and N withheld after flowering (N-)]. Values are means \pm standard error, $n = 15$.

Treatments		Boll parameters		
N	$[CO_2]$	Total bolls	Retained bolls	Retention
		no. plant ⁻¹		%
N+	Subambient	20.8 \pm 1.6	12.4 \pm 1.6	55.4 \pm 4.2
	Ambient	50.7 \pm 3.6	24.4 \pm 3.6	45.1 \pm 3.2
	Elevated	58.6 \pm 3.7	30.5 \pm 3.7	49.4 \pm 3.1
N-	Subambient	26.4 \pm 1.2	12.1 \pm 1.2	44.2 \pm 2.6
	Ambient	39.1 \pm 2.2	16.1 \pm 2.2	38.8 \pm 3.4
	Elevated	47.1 \pm 3.7	19.8 \pm 3.7	37.4 \pm 4.5
ANOVA	$[CO_2]$	***	***	NS†
	N	***	**	***
	$[CO_2] \times N$	***	*	NS

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† NS, not significant at the 0.1 probability level.

subambient $[CO_2]$ to ambient $[CO_2]$ and from ambient $[CO_2]$ to elevated $[CO_2]$ were observed at both N+ and N- conditions. This is because the growth response of the inherently plastic and indeterminate cotton plant was more limited by C than N, resulting in distribution of the acquired N over the larger biomass for plants grown in elevated $[CO_2]$ environments. We found that the decrease in leaf N was more for elevated $[CO_2]$ -grown plants compared with plants grown at ambient $[CO_2]$ and subambient $[CO_2]$ conditions (Fig. 1). Leaf N response in cotton depends on C gain at different atmospheric $[CO_2]$. Our results are in agreement with the prior reports where decreases of leaf N concentration were reported from ambient to elevated $[CO_2]$ for wheat (*Triticum aestivum* L.) and cotton (Rogers et al., 1993, 1996b; Booker, 2000) and rice (*Oryza sativa* L.) (Ziska et al., 1996). These reductions were observed when leaf N was expressed both on a dry weight or area basis (Rogers et al., 1996b). Cotrufo et al. (1998) summarized the impacts of elevated $[CO_2]$ and N on plant tissues and showed 14% reduction in plant tissue N under elevated $[CO_2]$ similar to our results presented here.

An increase in plant growth and development, in terms of increased plant height and mainstem nodes, was observed early in elevated $[CO_2]$ environments due to positive effects of both C and N. Similar plant height increases due to elevated $[CO_2]$ were reported in soybean (Allen et al., 1991). We observed that the production of vegetative and fruiting branches depended on the availability of C and N resources as evidenced by increased branch numbers at the elevated $[CO_2]$ and N+ treatment. Increased branch growth and development observed in cotton are similar to increased tillering in rice (Aben et al., 1999) and greater tuber initiation in potato (*Solanum tuberosum* L.) (Heineke et al., 1999) under elevated $[CO_2]$ conditions. Reddy et al. (1998) showed that the branches were produced in response to tissues rich in carbohydrates in cotton at a range of temperature conditions.

Cotton being indeterminate in growth habit exhibits simultaneous vegetative growth and reproductive development. Similar to branch production, boll production

Table 4. Leaf, stem, root, boll, total, and aboveground dry matter production and partitioning of cotton plants grown at subambient, ambient, and elevated levels of carbon dioxide concentration ($[\text{CO}_2]$) (180, 360, and 720 $\mu\text{mol mol}^{-1}$, respectively) at two levels of N [continuous N throughout the plant growth (N+) and N withheld after flowering (N-)]. Values are means \pm standard error, $n = 15$.

Treatments		Dry matter production						Root/shoot ratio
N	[CO ₂]	Total	Aboveground biomass	Leaf	Stem	Root	Boll	
g plant ⁻¹								
N+	Subambient	195.9	184.9 ± 25.6	50 ± 7.0	63.9 ± 8.4	10.97	71.0 ± 9.5	0.059
	Ambient	291.8	278.1 ± 38.5	61.2 ± 6.6	116.9 ± 13.0	13.7	120.1 ± 18.5	0.049
	Elevated	382.9	362.6 ± 34.3	67.3 ± 6.3	135 ± 8.5	20.3	163.9 ± 25.4	0.056
N–	Subambient	165.2	152.6 ± 13.9	25.5 ± 2.5	62.2 ± 5.9	12.5	65.0 ± 6.1	0.082
	Ambient	233.3	215.4 ± 28.4	30.1 ± 4.2	91.5 ± 11.8	17.9	93.8 ± 13.6	0.083
	Elevated	309.1	288.8 ± 47.5	39.7 ± 5.9	127.9 ± 19.7	20.3	121.2 ± 22.7	0.070
ANOVA	[CO ₂]	†	***	*	***	†	***	
	N		**	***	NS		*	
	[CO ₂] × N		NS‡	NS	NS		NS	

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Statistical analysis was not carried out as roots were harvested from the entire soil bin and not for each plant individually.

‡ NS, not significant at the 0.1 probability level.

also depended on both C and N resources; therefore, plants grown under elevated $[\text{CO}_2]$ and N+ conditions had more bolls than plants grown under other treatments. When N was limiting (elevated $[\text{CO}_2]$ and N-), the percentage increase was reduced. The plants inability under N- conditions to fully satisfy the assimilate requirements of growing bolls was shown by a reduced number of retained bolls, but the size of the retained boll was not affected by either $[\text{CO}_2]$ or N supply. Thus, the increased boll dry weight observed under elevated $[\text{CO}_2]$ and N+ condition was due to greater number of retained bolls and not due to increased individual boll dry weights. Elevated $[\text{CO}_2]$ increased both vegetative and reproductive biomass compared with ambient $[\text{CO}_2]$ and subambient $[\text{CO}_2]$. The mechanism by which the crop partitions its growth is complex. Plants grown at elevated $[\text{CO}_2]$ possessed larger root systems as was evident by increased root dry weight. Plants grown at elevated $[\text{CO}_2]$ had both increased aboveground and root biomass. Increased photosynthesis will result in greater amounts of metabolites available for growth as seen in many studies including cotton (Kimball et al., 2002; Reddy et al., 2000). Similar results were observed in experiments conducted with open-top (Kimball and

Mauney, 1993) and FACE experiments (Mauney et al., 1994; Pinter et al., 1996).

Despite decades of research on N effects on crop growth and development (Gerik et al., 1998), studies on quantitative fiber quality responses to N are still missing. Fiber growth and development are dynamic traits that change throughout a long period of boll growth and development (Seagull et al., 2000), and environmental and management factors during this period can potentially modify the fiber properties (Bradow and Davisonis, 2000; Reddy et al., 1999). In this study, fiber quality parameters surprisingly followed upward/downward trends with leaf N-BMP irrespective of $[\text{CO}_2]$ treatments. Under N+ conditions, atmospheric $[\text{CO}_2]$ did not affect any of the fiber properties similar to the observations of Reddy et al. (1999) in an experiment conducted under optimum water and nutrient conditions under a range of temperature conditions. Increased $[\text{CO}_2]$ caused lower leaf N concentrations, and reductions in leaf N were more pronounced under elevated $[\text{CO}_2]$ and N- conditions. The reduced leaf N concentrations, in turn, affected fiber quality directly, showing that CO_2 had an indirect effect on fiber quality. Our results indicate that under conditions of optimum N, atmospheric

Table 5. Boll, boll component dry weights, and seed number per boll of cotton plants grown at subambient, ambient, and elevated levels of carbon dioxide concentration ($[\text{CO}_2]$) (180, 360, and 720 $\mu\text{mol mol}^{-1}$, respectively) at two levels of N [continuous N throughout the plant growth (N+) and N withheld after flowering (N-)]. Values are means \pm standard error, $n = 15$.

Treatments		Boll and boll component dry weights				
N	[CO ₂]	Boll	Burr	Seed	Lint	Seeds
		g boll ⁻¹				no. boll ⁻¹
N+	Subambient	5.81 ± 0.17	1.24 ± 0.05	2.90 ± 0.09	1.67 ± 0.05	33.9 ± 0.67
	Ambient	4.83 ± 0.19	1.17 ± 0.04	2.22 ± 0.09	1.44 ± 0.06	29.9 ± 1.2
	Elevated	5.25 ± 0.21	1.26 ± 0.05	2.49 ± 0.10	1.50 ± 0.06	32.9 ± 0.59
N–	Subambient	5.56 ± 0.13	1.14 ± 0.02	2.67 ± 0.08	1.76 ± 0.05	31.5 ± 0.81
	Ambient	5.78 ± 0.14	1.24 ± 0.04	2.76 ± 0.07	1.78 ± 0.05	32.3 ± 0.42
	Elevated	5.59 ± 0.18	1.23 ± 0.05	2.67 ± 0.08	1.70 ± 0.08	32.4 ± 0.8
ANOVA	[CO ₂]	NS†	NS	**	NS	NS
	N	*	NS	*	***	NS
	[CO ₂] × N	**	NS	***	NS	***

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† NS, not significant at the 0.1 probability level.

[CO₂] will likely cause no effect on fiber quality. Our results also show that fiber quality is very sensitive to N supply, and if N is limiting, plants grown in elevated [CO₂] may produce less desirable fiber. This may be due to the less production of growth regulators required for fiber development at low N concentrations. It was suggested that indole acetic acid (IAA), which is produced in response to N fertilization, plays an important role in fiber production (Beasley and Ting, 1974; Nathani et al., 1982; Gokhani and Thaker, 2002). This can be due to the requirement of N in the production of the enzyme systems of IAA synthesis (Bulatova and Pomaz, 1984). Sims et al. (1998) showed reductions in photosynthetic enzyme synthesis due to reduced availability of N under N-limited conditions.

Fiber length parameters such as mean fiber length showed a quadratic trend with leaf N-BMP and increased as leaf N-BMP increased. In contrast, some studies showed that N had a very little effect on fiber length and strength (Ebelhar and Welch, 1996; Bauer et al., 1993). Short fiber content is gaining importance as an important fiber-processing component; and our results show higher SFC in plants with lower leaf N-BMP. When the bolls begin to grow, fiber cells on the seed coat begin to elongate for about 3 wk, and lower leaf N conditions during this time reduce the fiber length (Constable and Hearn, 1981; Perkins and Douglas, 1965), which might have been the cause of higher SFC. Similarly, water deficits (Hearn, 1994b) and temperatures (Reddy et al., 1999) during the fiber elongation phase are shown to affect fiber length and SFC.

Fiber maturity parameters such as θ and A(n) showed negative trends with leaf N-BMP. Increased leaf N-BMP resulted in lower μ AFIS than is normally acceptable by the mills. Micronafis is AFIS-calculated micronaire and closely correlated with the micronaire reading (Calhoun et al., 1997). The micronaire readings reflect a composite of fiber maturity and fineness characteristics. As leaf N-BMP increased, θ and A(n) decreased. After the fiber elongation phase, a layer of cellulose is deposited daily on the inside of the cotton fiber. Secondary wall thickening then occurs and directly corresponds to the fiber strength and micronaire (Ramey, 1986; Seagull et al., 2000). Nitrogen stress during this phase of fiber development was shown to have detrimental effects on cotton fiber quality. Optimum N levels were required to produce μ AFIS values in an acceptable range (3.5 to 4.9 according to USDA-AMS office). Micronaire management is a new concept requiring a more thorough understanding of the causes of high and low micronaire readings. Both high and low micronaire readings affect many growers in the USA and other cotton-producing regions of the world (Hearn, 1976; Rochester et al., 2001). Reddy et al. (1999) showed that plants grown in high temperatures and ambient [CO₂] produced fibers with low μ AFIS, θ , and A(n). Fiber fineness parameters such as FFF had a positive trend with leaf N-BMP. When the IFF was >14%, it was classified as *high* and is not within the acceptable limits of the industry (Williams and Yankey, 1996), and an increase in leaf N-BMP increased IFF in our experiment.

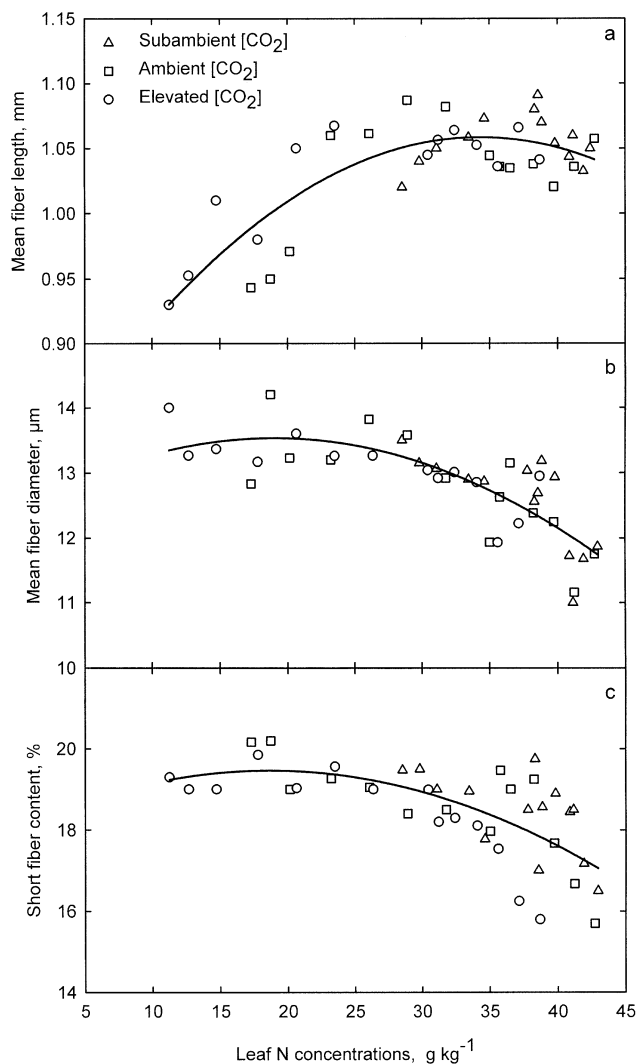


Fig. 2. Fiber length, diameter, and short fiber content as a function of leaf N concentrations (g kg^{-1}) during the boll maturation period in cotton. Observations are from plants that were grown under three levels of carbon dioxide concentrations ([CO₂]), two levels of N, and seven groups of bolls grouped based on flowering dates. Fitted regressions are (a) $y = -0.0003x^2 + 0.0224x + 0.6968$, $r^2 = 0.63$, $n = 42$ for mean fiber length (mm); (b) $y = -0.0031x^2 + 0.118x + 12.394$, $r^2 = 0.61$, $n = 42$ for mean fiber diameter (μ); and (c) $y = -0.005x^2 + 0.189x + 17.647$, $r^2 = 0.50$, $n = 42$ for short fiber content (%).

The lower quality of fiber observed for plants grown under low N concentrations and the higher quality of fiber at optimum N conditions were due to the flux of carbohydrate supply during boll development as positive correlations were observed between photosynthesis and fiber quality (Pettigrew, 1995, 2001; Tewolde and Fernandez, 2003). In contrast, some studies showed that the N effect on fiber properties was not significant (Phipps et al., 1997; Elayan, 1992; Sawan et al., 1997; Bauer et al., 1993). Imposing a moderate level of N deficiency as a management strategy to selectively suppress excess vegetative growth and enhance maturity as discussed by Tewolde et al. (1994) may therefore be a plausible practice without affecting the quality of the fiber produced.

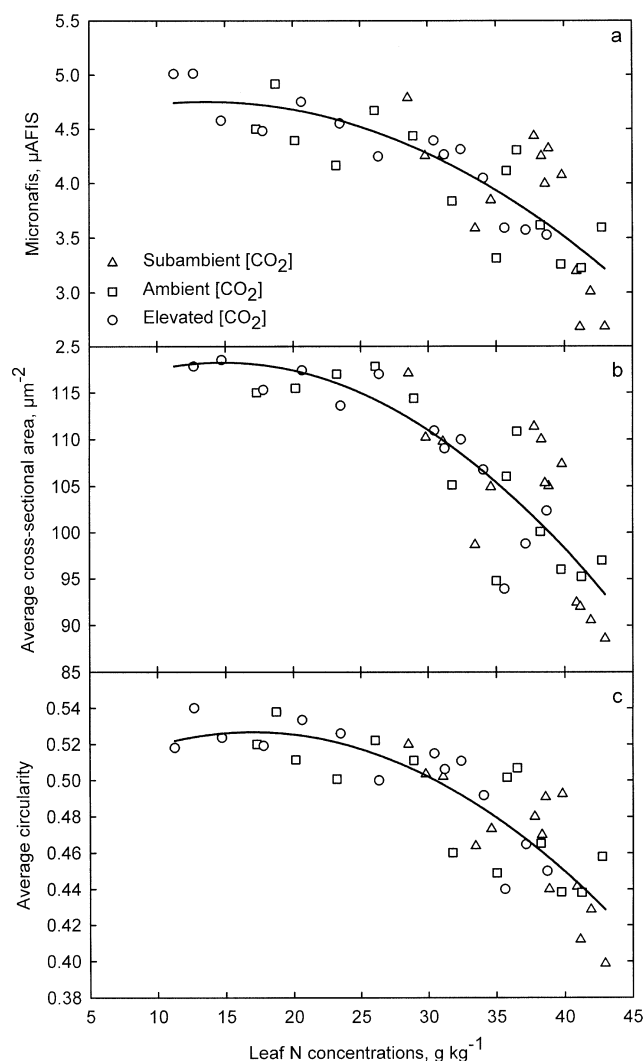


Fig. 3. Micronafis (μAFIS), cross-sectional area, and circularity as a function of leaf N concentrations (g kg^{-1}) during the boll maturation period in cotton. Observations are from plants that are grown under three levels of carbon dioxide concentrations ($[\text{CO}_2]$), two levels of N, and seven groups of bolls grouped based on flowering dates. Fitted regressions are (a) $y = -0.002x^2 + 0.0612x + 4.2543$, $r^2 = 0.65$, $n = 42$ for micronafis; (b) $y = -0.0387x^2 + 1.335x + 105.8$, $r^2 = 0.76$, $n = 42$ for average cross-sectional area (μm^2); and (c) $y = -0.0002x^2 + 0.0069x + 0.4545$, $r^2 = 0.74$, $n = 42$ for average circularity (θ).

Our results show a positive impact of elevated $[\text{CO}_2]$ on cotton biomass production, but N availability will affect the magnitude of the response, and optimum N will allow cotton plants to produce more fiber with good quality. The existing critical N values, which were actually established when $[\text{CO}_2]$ was considerably lower ($330 \mu\text{mol mol}^{-1}$) than the current levels (Reuter et al., 1997), require reconsideration as atmospheric $[\text{CO}_2]$ is steadily increasing. The mineral requirements of plants grown in high $[\text{CO}_2]$ environments and predicting nutrient requirements of plants in such environments may be more complicated than expected. Careful consideration of N fertilization will be necessary to take full advantage of any future increases in atmospheric $[\text{CO}_2]$.

To date, quantitative relationships between various

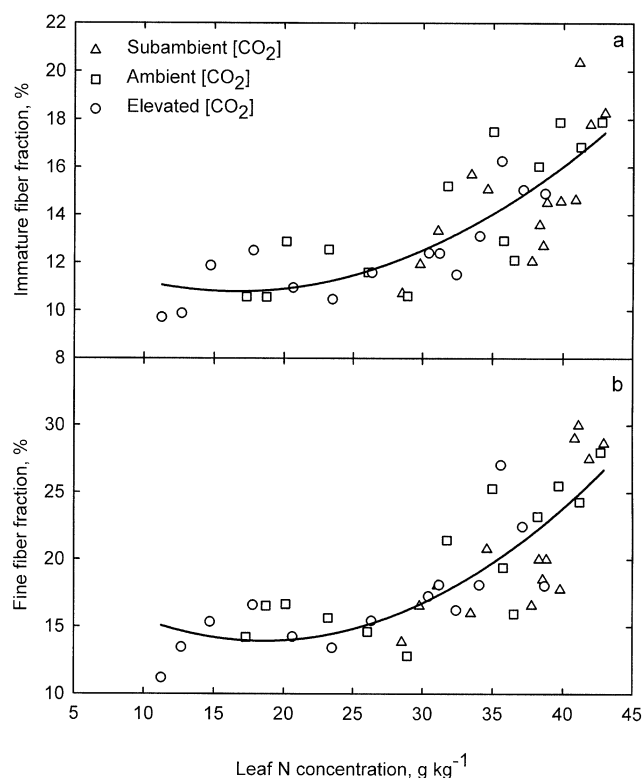


Fig. 4. Immature fiber fraction and fine fiber fraction as a function of leaf N concentrations (g kg^{-1}) during the boll maturation period in cotton. Observations are from plants that are grown under three levels of carbon dioxide concentrations ($[\text{CO}_2]$), two levels of N, and seven groups of bolls grouped based on flowering dates. Fitted regressions are (a) $y = 0.0102x^2 - 0.3354x + 13.487$, $r^2 = 0.65$, $n = 42$ for immature fiber fraction (%), and (b) $y = 0.019x^2 - 0.662x + 19.744$, $r^2 = 0.67$, $n = 42$ for fine fiber fraction (%).

fiber parameters of cotton as a function of leaf C and N are not available for developing models to study current and projected changes in $[\text{CO}_2]$ and its interaction with other nutrients (Reddy et al., 2002a). Since none of the fiber parameters were directly affected by varying $[\text{CO}_2]$ and thus C under optimum N conditions, and all the fiber characteristics varied as a function of leaf N-BMP, developing N-specific reduction factors or indices from the data as shown in Fig. 2–4 provides the functional algorithms needed to develop a model for fiber quality for N. The developed response functions, if incorporated into process-level simulation cotton models such as GOSSYM, will enhance the applicability of the cotton model as a management decision aid (Reddy et al., 2002b). If we could model fiber quality properties with weather and management practices during the fiber growth period, farm managers and textile firms could predict the fiber quality well in advance, and the entire marketing process could proceed with prior knowledge of fiber quality. Varietal and abiotic constraints are also needed to simulate fiber parameters in production environments. Also, models can be used to manage cotton not only to maximize seed cotton yield but also to optimize fiber quality during the crop growing season by appropriate management decisions without jeopardizing environmental effects on cotton production under both present and future climatic conditions.

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